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Yield potential and yield stability of Argentine maize hybrids over 45 years of breeding

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ABSTRACT

Maize (*Zea Mays* L.) grain yield have increased during the last decades and there is an ample range of rates of grain yield increments reported in the literature. Maize hybrids comparison at their optimum plant density might contribute to elucidate the yield potential increments during the last decades. In addition, high plant density testing and multi-location trials in modern breeding programs might have contributed to greater stress tolerance in modern hybrids. Then, a close relationship between tolerance to high plant density and yield stability in hybrids released in different decades is expected. The objectives of this study were (i) to determine the optimum plant density and the gain in yield potential and its components, and (ii) to test the hypothesis that tolerance to high plant densities and yield stability are strongly associated, for Argentinean maize hybrids released between 1965 and 2010. One set of experiments was conducted at Balcarce, Argentina during five growing seasons (Exps. 1–5), each experiment included a combination of plant densities (1.5–20 plants m^{-2}) and hybrids released in different years (1965–2010). Data from these experiments were used to estimate optimum plant density, gains in yield potential and tolerance to high plant density. Another experiment (Exp. 6) included 18 trials conducted in a wide range of environments and data from these trials were used to estimate yield stability. The optimum density to attain the maximum yield ranged from 9.7 to 16.4 pl m^{-2} and it did not present a clear trend with the year of hybrid release. Yield potential increased at a rate of 0.83% or 107 kg ha^{-1} $year^{-1}$ ($p < 0.001$) and yield increments were attributed mainly to gains in kernel number per unit area and to biomass production steady increments during the 1965–2010 period. Harvest index contributions to yield increments were important for the period 1980–1993, but HI remained stable during the last two decades. Yield stability increased with the year of hybrid release, in accordance with higher mean yields and lower CV (coefficient of variation) across environments of modern compared with older hybrids. Tolerance to high plant densities increased during the last 45 years and it was direct and significantly associated with yield stability, providing strong bases for the use of high plant densities as a method to attain gains in yield stability.

1. Introduction

Maize (*Zea mays* L.) grain yield has increased at a rate of 110 kg ha^{-1} $year^{-1}$ between 1965 and 2014 in Argentina (FAOSTAT, 2016) and this increment was attributed to genetic gains, the improvement of management practices and an interaction between these two factors (Eyherabide et al., 1994). Genetic gain in grain yield ranged from 74 to 170 kg ha^{-1} yr^{-1} for different time periods between 1930–2004, in the US corn belt, Argentina and Brazil (Cunha Fernandes and Franzon, 1997; Duvick, 2005; Eyherabide et al., 1994; Eyherabide and Damilano, 2001). In particular, genetic gain in yield potential (i.e. when hybrids were grown in environments to which they are adapted and with no resource availability limitations) ranged from 132 to 166 kg ha^{-1} yr^{-1} in Argentina between 1965 and 1997 (Echarte et al., 2000; Luque et al., 2006). Genetic gains in yield potential ranged from null to as high as 196 kg ha^{-1} yr^{-1} for hybrids released in USA from 1985 (Campos et al., 2006). Contrasting results among studies could be related

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to the sampling method (i.e. machine- vs. hand-harvested crops), the approach to calculate genetic gain (i.e. average yield at different plant densities vs. yield at optimum plant density), the period under study and the interaction between genotype and environment (Tollenaar and Lee, 2002).

Comparison of hybrids released at different decades at their optimum plant density (D_{op}) should better reflect the genetic yield potential increments with the year of hybrid release. The response of maize grain yield to plant density (D) is curvilinear and the plant density that results in the highest grain yield is defined as the optimum plant density for grain yield. Maize hybrids differ in their response to plant density (Echarte et al., 2000; Sangoi et al., 2002). In Argentina, hybrids released in the 1990s out-yielded older ones in a wide range of plant densities (Echarte et al., 2000; Luque et al., 2006). In contrast, little or no increments in grain yield at low plant densities were reported for the US corn belt hybrids (Duvick and Cassman, 1999; Tollenaar and Wu, 1999). In France, the optimum plant density increased about 0.96 plants m^{-2} every 10 years for the 1950–1985 period (Derieux et al., 1987); and similar optimum plant density increments were reported for the U.S. Corn Belt for the 1920–1980 period (Russel, 1984). In addition, (Tollenaar, 1989) reported higher optimum plant densities for 1980s hybrids than for hybrids released in the 1950s.

During the last decades, breeding programs have increased the plant densities at which they test hybrid performance (Tokatlidis and Koutroubas, 2004; Troyer, 1996). In particular, plant density used in breeding programs in Argentina were 4 plants m^{-2} in the 1960s and 8.5 plants m^{-2} currently (Eyherabide et al., 1994). Therefore, higher optimum plant density might be expected in modern than in older maize hybrids. In addition, modern breeding programs test inbred lines and hybrids in a large number of locations (Troyer, 1996). It has been suggested that this type of maize testing (i.e. high plant density and multi-location trials) has contributed to stress tolerance in modern maize hybrids (Tokatlidis and Koutroubas, 2004; Troyer, 1996). Accordingly, performance of hybrids at high plant density (Duvick et al., 2004; Echarte et al., 2000; Tollenaar and Lee, 2002), low soil N availability (Echarte et al., 2008; Rajcan and Tollenaar, 1999), and low soil water availability (Duvick and Cassman, 1999; Nagore et al., 2014) was better in modern than in older maize hybrids. A close relationship between tolerance to high plant density and yield stability across hybrids released in different decades is expected. To the best of our knowledge there is no report in the literature testing this hypothesis.

The objectives of this study were (i) to determine the optimum plant density and the gain in yield potential, and (ii) to test the hypothesis that tolerance to high plant densities and yield stability are strongly associated, in Argentinean maize hybrids released between 1965 and 2010.

2. Material and methods

2.1. Optimum plant density and yield potential

2.1.1. Site and crop management

Crops were grown at Balcarce, Argentina (37°45′S, 58°18′W; elevation 130 m) during 1996–1997 (Exp. 1), 1998–1999 (Exp. 2), 2009–2010 (Exp. 3), 2010–2011 (Exp. 4) and 2012–2013 (Exp. 5). The soil was a Typic Argiudoll with a depth of 1.5 m and with 5.6% topsoil organic matter. Hybrids were sown on October 10 (Exp. 1), October 15 (Exp. 2), October 14 (Exp 3), October 20 (Exp 4) and October 24 (Exp 5). Crops were fertilized with 35 kg P ha^{-1} before sowing and with 150 kg N ha^{-1} at V6 (Ritchie and Hanway, 1982). These rates were calculated using locally adjusted models based on soil analysis and target yield for modern maize hybrids (Barbieri et al., 2008). Soil water to 1 m depth was kept over 60% of available water by sprinkler irrigation in all experiments. Weeds and insects were adequately controlled. Mean temperature and mean daily incident photosynthetically active radiation per month from October to April of each experiment are shown in Table 2; average silking dates were January 14th, 6th, 6th, 14th, 10th for Exps. 1–5, respectively.

2.1.2. Plant material and experimental design

Table 1 shows hybrids used in each experiment and their characteristics. Hybrids selected for this study were among the eight most cultivated hybrids in the Argentinean Pampas for at least 5 years after their release. In addition, seven of the eight hybrids were developed by Dekalb-Monsanto, which had a high level of participation in the Argentinean market since its introduction; and currently has more than 50% of the market. In Exps. 1 and 2, the experimental design was a split plot randomized complete-block with three replications, in which plant density treatments were assigned to main plots and hybrids to subplots. In Exps. 3–5, the experimental design was a randomized complete-block design with three replications.

Plant densities were 5, 8, 11 and 14.5 plants m^{-2} in Exp. 1; 2, 4, 8 and 16 plants m^{-2} in Exp. 2; 5, 9.5, and 14 plants m^{-2} in Exps. 3 and 4 and 8, 14 and 20 plants m^{-2} in Exp. 5. Plots were over-sown and thinned to the desired densities at V3 (Ritchie and Hanway, 1982). Subplots comprised 4–7 rows, 7 m long in Exps. 1 and 2 and plots comprised 4 rows, 10 m long in Exps. 3, 4 and 5. Rows were 0.7 m apart in all the experiments.

2.1.3. Measurements

Grain yield per plant (Yp) and shoot dry matter per plant (Bp) were determined at physiological maturity; samples of 10–30 individual plants (depending on the plant density) were collected from the two central rows of each plot in a 3 m^{-2} area. Sample areas were bordered by at least 2 guard rows and at least 1 m in the row. Each plant was oven-dried (forced air at 65 °C) to constant weight, and weighed. Dry individual ears were separated from the plant and shelled. Grain yield per plant and its components were determined by counting and weighing all the kernels per uppermost and second ear. Individual kernel weight was calculated as kernels weight per ear divided by kernel number per ear; and values from all the plants in a plot were averaged to obtain mean individual kernel weight per plot. Grain yield results were expressed at 0% humidity.

2.1.4. Data analysis

Optimum plant density was estimated using a modified version of (Sarlangue et al., 2007) methodology; this methodology was chosen to obtain a more precise estimation of D_{op}. Poor estimates of D_{op} might be expected when fitting a quadratic function to the relationship between grain yield and plant density; since the degree of curvilinearity might be different at both sides of D_{op} due to distinctive processes affecting yield at low and at high plant densities (Echarte et al., 2004).

To calculate D_{op}, (i) the relationship between Bp and D was fitted with Eq. (1); this was done for each hybrid and experiment, since dry matter production is highly influenced by the environmental conditions (Aguilar and López-Bellido, 1996).

$$Bp = a_1 + (\mathrm{Bmax} - a_1) * \left[1 - e^{\left(-b_1 * \frac{1}{D} \right)} \right] \quad If\ Bp > 0 \tag{1}$$

This equation presents biologically meaningful parameters. Thus, *a1* is the intercept of the function and it represents the minimum ground area per plant required to produce shoot biomass; *b1* is the degree of curvature of the function; *B*max is the maximum

Table 1

Monthly mean daily temperature and daily incident photosynthetic active radiation (PAR) from October (O) to April (A) for Experiments 1–5 and percentile 25 and 75 for a 30 year period at Balcarce (1984–2014).

Exp.	Mean temperature (°C)							Daily incident PAR (MJ m^{-2})						
	O	N	D	J	F	M	A	O	N	D	J	F	M	A
1	14.2	17.0	19.0	22.3	18.6	18.0	15.6	7.7	10.1	9.9	10.9	9.9	7.6	5.0
2	13.2	15.7	17.1	19.7	18.2	18.1	15.5	6.9	8.9	9.9	11.1	8.6	7.9	3.9
3	13.9	17.1	19.1	22.9	20.3	18.5	14.3	8.8	10.0	10.8	11.0	9.6	6.6	5.7
4	13.7	16.2	20.9	22.2	20.1	19.8	16.2	8.2	10.3	12.5	11.4	10.1	8.1	5.7
5	14.9	17.7	20.2	21.1	21.1	16.3	17.2	8.1	10.6	10.7	9.9	10.1	7.4	4.7
Percentile 25	12.9	15.6	18.1	20.3	19.1	17.5	13.9	7.8	10.1	11.0	11.1	9.6	7.3	5.0
Percentile 75	13.8	16.7	19.5	21.0	20.4	18.2	14.8	8.3	10.6	11.5	11.5	10.2	7.8	5.5

Table 2

Hybrids used in each experiment and their characteristics (i.e. breeding company, year of release, cross type, endosperm type and relative maturity).

Hybrid	Company	Experiments						Year of release	Cross type	Endosperm type	Relative Maturity
		1	2	3	4	5	6				
DKF880	Dekalb	x				x	x	1965	Double	Flint	120
M400	Morgan	x	x					1978	Double	Flint	128
DK4F36	Dekalb	x	x					1982	Double	Flint	127
DK752	Dekalb	x	x				x	1993a	Single	Semi-dent	125
DK664	Dekalb	x	x				x	1993b	Single	Semi-dent	116
DK664 MG	Dekalb			x	x	x		1993b	Single	Semi-dent	116
DK682 MG	Dekalb			x	x			2000	Single	Semi-dent	118
AW190 MG	Dekalb			x	x			2003	Single	Semi-dent	119
DK692 MG	Dekalb			x	x	x		2010	Single	Semi-dent	119
DK 692 RR2	Dekalb						x	2010	Single	Semi-dent	119
DK 7210 VT3P	Dekalb						x	2012	Single	Semi-dent	122

biomass attainable per plant, and *1/D* is the ground area occupied by each plant, which is related to the resource availability per plant.

(ii) The relationship between Yp (including first and second ear) and Bp was fitted with an hyperbolic function with an intercept in the x axis (Eq. (2)).

$$Yp = 0 \quad If\ Bp \le Bt$$

$$Yp = \frac{a_2\,(\mathrm{Bp} - \mathrm{Bt})}{1 + \mathrm{b}_2\,(\mathrm{Bp} - \mathrm{Bt})} \quad If\ Bp > Bt \tag{2}$$

Where a_2 is the initial slope of the relationship; *Bt* (g plant^{-1}) is the threshold aboveground biomass below which there is no grain yield; b_2 is the degree of curvilinearity of the relationship, and low values of b_2 indicate that the curve approaches a straight line.

(iii) A relationship between Yp and plant density was obtained by combining Eq. (1) and Eq. (2) (Eq. (3)); and Eq. (3) was multiplied by D (Eq. (4)) to obtain the relationship between grain yield per unit area (Y) and D.

$$Yp = \frac{a_2 \left\{ \left[\mathrm{a}_1 + (\mathrm{Bmax} - \mathrm{a}_1) * \left(1 - e^{\left(-\mathrm{b1} * \frac{1}{D} \right)} \right) \right] - \mathrm{Bt} \right\}}{1 + \mathrm{b}_2 \left\{ \left[\mathrm{a}_1 + (\mathrm{Bmax} - \mathrm{a}_1) * \left(1 - e^{\left(-\mathrm{b1} * \frac{1}{D} \right)} \right) \right] - \mathrm{Bt} \right\}} \tag{3}$$

$$Y = \frac{a_2 \left\{ \left[\mathrm{a}_1 + (\mathrm{Bmax} - \mathrm{a}_1) * \left(1 - e^{\left(-\mathrm{b1} * \frac{1}{D} \right)} \right) \right] - \mathrm{Bt} \right\}}{1 + \mathrm{b}_2 \left\{ \left[\mathrm{a}_1 + (\mathrm{Bmax} - \mathrm{a}_1) * \left(1 - e^{\left(-\mathrm{b1} * \frac{1}{D} \right)} \right) \right] - \mathrm{Bt} \right\}} * D \tag{4}$$

(iv) Optimum plant density ($\mathrm{D_{op}}$) for each combination of hybrid and experiment was obtained by setting to zero the first derivative of Eq. (4). Then yield at Dop (YP) was calculated with Eq. (4).

Plant biomass per unit area (B) at $\mathrm{D_{op}}$ was estimated by replacing D with $\mathrm{D_{op}}$ in Eq. (1) and multiplying by $\mathrm{D_{op}}$. Harvest index (HI) was estimated by dividing grain yield by plant biomass, both at $\mathrm{D_{op}}$. Kernel number per unit area (KN) at $\mathrm{D_{op}}$ was estimated from the quadratic or negative exponential function (depending on the best fit; $p < 0.05$ in all cases, not shown) fitted to the relationship between KN and plant density. Kernel weight at $\mathrm{D_{op}}$ was estimated from a linear KW response to increasing density ($p < 0.05$ in all cases, not shown).

Data of YP, its components (KN and KW), B and HI of each hybrid were relativized with respect to the mean yield of hybrid DK664 (100%), and they were combined across experiments. The two versions of the hybrid DK664 (DK664 and DK664MG) were considered as one same hybrid since (i) weeds and insects were adequately controlled, (ii) the two versions presented similar grain yield, grain yield components and phenology when were sown at one plant density in the same season (not shown); similar results were obtained in other Dekalb isogenic hybrid in terms of grain yield, kernel number and kernel weight (Laserna et al., 2012), and (iii) parameters of the relationships Bp − 1/D (Eq. (1)) and Yp − Bp (Eq. (2)) were similar between DK664 and DK664MG ($p > 0.05$, not shown). Linear regressions were fitted to the relationships between relative values of YP, KN, KW, B and HI as a function of the year of hybrid release; and their average change per year was estimated as the slope of the relationship in relative values (%) and in absolute values by multiplying the relative values with the mean yield of hybrid DK664.

2.2. Yield stability and tolerance to high plant density

2.2.1. Site and crop management

Five hybrids were grown at 18 locations across a wide range of environmental conditions in the Argentinean Pampas during 2012–2013 season (Exp. 6; Table 3). Field experiments were conducted under rain-fed conditions, crops were fertilized with 120 kg triple superphosphate Ca $(H_2PO_4)_2$ ha^{-1} and 140 kg N ha^{-1} before sowing, and weeds and insects were adequately controlled. Table 3 shows soil type and precipitation during the growing season and the dates of sowing, silking and physiological maturity at each location.

Table 3
General information on location, crop phenology and weather for the environments included in Exp. 6. Location: Name of location, Province (PV), Latitude (Lat), Longitud (Lg.), Soil type and Texture. Crop Phenology: Sowing, silking and Physiological Maturity (PM) dates. Weather: precipitation (PP) from sowing to physiological maturity (S-PM) and during January and February (J-F), which are considered the most critical months for grain yield production.

Location	PV[a]	Lat	Lg.	Soil Type[b]/Texture[c]	Sowing date	Silkingdate	PM date	PP S-PM (mm)	PP J-F (mm)	EI ($Mg\ ha^{-1}$)
Alcira	CBA	−32.8	−64.3	Udt Hpt/Sd Lm	17/10/12	07/01/13	18/03/13	553.0	138.9	6.30
Arias	CBA	−33.6	−62.5	Typ Arg/Lm	12/10/12	02/01/13	23/03/13	773.0	111.6	11.20
Azul	BA	−37.2	−59.8	Typ Hpd/Lm	20/11/12	08/02/13	20/04/13	596.0	100.8	6.20
Balcarce	BA	−37.9	−58.5	Typ Arg/St Lm	20/11/12	07/02/13	10/05/13	652.0	185.0	8.45
General Villegas	BA	−35.0	−63.2	Ent Hpd/Sd Lm	01/11/12	16/01/13	10/03/13	294.0	27.0	6.75
General Villegas	BA	−35.0	−63.2	Typ Arg/Lm	11/12/12	24/02/13	04/05/13	320.0	27.0	8.10
Junin	BA	−34.6	−61.0	Tpc Arg/St Lm	13/10/12	04/01/13	16/02/13	468.9	63.0	7.25
Laboulaye	CBA	−34.1	−63.3	Tpc Arg/Cl St Lm	24/10/12	11/01/13	02/03/13	342.9	47.3	11.48
Los Cardos	SF	−32.3	−61.6	Ent Hpt/St Lm	27/10/12	08/01/13	22/02/13	427.0	140.0	8.95
Maximo Paz	SF	−33.5	−60.9	Tpc Arg/Cl St Lm	07/11/12	21/01/13	10/03/13	479.0	169.0	5.54
Monte Buey	CBA	−32.8	−62.5	Tpc Arg/St Lm	26/10/12	09/01/13	24/02/13	293.0	106.0	8.57
Murphy	SF	−33.6	−61.8	Ent Hpt/Sd Lm	04/10/12	01/01/13	14/02/13	679.3	81.8	9.47
Necochea-QQ	BA	−38.4	−58.7	Ent Hpd/St Lm	18/11/12	02/02/13	30/04/13	437.0	85.0	5.34
Oliva	CBA	−32.0	−63.6	Udt Hpt/Sd Lm	18/10/12	25/12/12	20/02/13	327.0	187.0	6.71
QuemúQuemú	LP	−36.2	−63.6	Tpc Hpd/Lm	01/11/12	06/01/13	06/03/13	339.0	54.0	5.49
Rincon del N.	ER	−32.7	−59.9	Vrt Arg/St Lm	26/09/12	07/12/12	30/01/13	817.0	165.0	7.25
San Francisco	CBA	−31.4	−62.1	Aqc Arg/Cl St Lm	24/10/12	24/12/12	16/02/13	450.0	124.0	10.68
Tandil	BA	−37.4	−59.1	Udt Hpt/Sd Lm	17/11/12	01/02/13	01/05/13	513.0	73.8	7.21

[a] BA: Buenos Aires, LP: La Pampa, SF: Santa Fe, CBA: Córdoba and ER: Entre Ríos.
[b] Udt: Udortentic, Hpt: Haplustoll, Hpd: Hapludoll: Typ: Typic, Arg:Argiudoll, Ent: Entic, Vrt: Vertic, Aqc: Aquic.
[c] Sd: Sandy, Lm: loam, St: Silty, Cl: Clay.

2.2.2. *Plant material and experimental design*

Hybrids used in Exp. 6 and their characteristics are shown in Table 1. Each hybrid was representative of the Dekalb breeding program in Argentina and it was largely sown in the Argentinean Pampas after its release. The experimental design at each location was a split plot randomized complete-block with three replications, in which plant density treatments were assigned to main plots and hybrids to subplots. Plant densities were 5, 7, 9 and 11 plants m^{-2}. Experimental units comprised four rows, 10.2 m long and 0.52 m apart. The two versions of hybrid DK664 (i.e. DK664 and DK664MG) and of hybrid DK692 (i.e. DK692MG and DK692RR2) were considered one same hybrid based on the adequate control of weeds and insects, and also on their similar grain yield, grain yield components and phenology, when the two versions of the hybrids were available at the same location ($p > 0.05$; not shown).

2.2.3. *Measurements*

Grain yield was determined at physiological maturity by machine harvesting the whole area per plot. Grain yield was expressed at 0% humidity.

2.2.4. *Data analysis*

The environment at each location was characterized with an environmental index (EI) that resulted from the mean yield of all the hybrids at each location. The percentage variation of grain yield across EI due to genotype (G), environment (E) and GXE interaction was estimated from the ANOVA analysis, by dividing the sum of squares of each source of variation (i.e. G, E, GxE, repetitions and error) by the total sum of squares. Yield stability was estimated with two approaches, (i) the slope "b" of the linear regression fitted to the relationship between grain yield (i.e. the highest yield among the 4 densities) and EI for each hybrid (Finlay and Wilkinson, 1963), and (ii) the coefficient of variation (CV) for yield across locations (Francis and Kannenberg, 1978). The CV was calculated following Eq. (5):

$$CV_i = \frac{\sqrt{\frac{1}{E-1}\sum_{J=1}^{E}\left(y_{ij.} - y_{i.}\right)^2}}{y_{i.}}100\% \tag{5}$$

Where CVi is the coefficient of variation of the "i" hybrid, E represents the environments, yij. is the grain yield of the "i" hybrid in the "j" environment and yi. represents the mean yield of the "i" hybrid across the environments.

2.2.4.1. *Tolerance to high plant density was estimated also with two approaches.*

(i) as the grain yield lost (YL) between grain yield at D_{op} (Y D_{op}) and grain yield at two times D_{op} (Y $2D_{op}$) for each hybrid in absolute (YL, Eq. (6)) and relative (YL%, Eq. (7)) values.

$$YL = Y_{D_{op}} - Y_{2D_{op}} \tag{6}$$

$$YL\% = 100 - \left(\frac{Y_{2D_{op}}}{Y_{D_{op}}} * 100\right) \tag{7}$$

(ii) from the quadratic coefficient (β_2) of the second order polynomial function (Eq. (8)) fitted to the relationships between grain yield and plant density (Eq. (4)). The equation was fitted to the absolute (Eq. (8)) and relative (Eq. (9)) values of grain yield in the range from D_{op} to two times D_{op} ($2D_{op}$).

$$Y = B_0 + B_1 * D + B_2 * D^2 \tag{8}$$

$$Yr = B_0 + B_1 * D_r + B_2 * {D_r}^2 \tag{9}$$

Where Y and D are grain yield and plant density, respectively; Yr is the relative yield with respect to Y D_{op}, D_r is the relative density with respect to D_{op} and $B_{0,}$ B_1 and B_2 are the origin, the initial slope and the quadratic coefficient of the function. β_2 is associated with the rate of decrease of Y when D increases from D_{op} (i.e. from D_{op} to $2D_{op}$). Larger negative values of B_2 represent larger yield reductions when doubling plant density from D_{op}.

The association between indices that characterize tolerance to high plant density (i.e. B_2 and *relative* B_2) and yield stability (CV) was studied with regression analyses. Hybrids included in this analysis (DKF880, DK664, DK752 and DK692) had information on yield response to plant density and on yield stability.

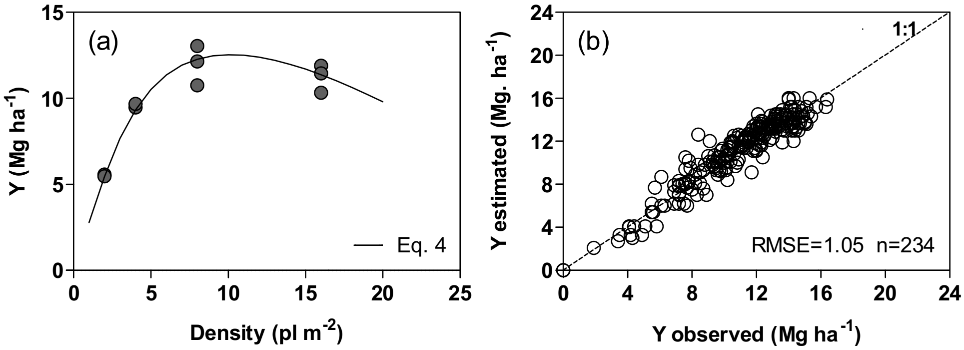

Fig. 1. (a) Grain yield (Y) in response to plant density and fitted Eq. (4) (solid line); example for one hybrid in one experiment (i.e. DK664 in Exp. 2), (b) Estimated Y with Eq. (4) as a function of observed Y for each combination of replication, density, hybrid and experiment for all the hybrids in Exps. 1–5. RMSE, root mean square error.

Table 4
Optimum plant density (D_{op}) and yield potential, shoot biomass production (B), harvest index (HI), kernel number per unit area (KN) and kernel weight (KW), at optimum plant density for each combination of hybrid and experiment. Data from Exps. 1–5.

Experiment	Year of hybrid release	Season	D_{op}	Yield potential	B	HI	KN	KW
			$Pl\ m^{-2}$	$g\ m^{-2}$	$g\ m^{-2}$	$g\ m^{-2}$/ $g\ m^{-2}$	$kernel\ m^{-2}$	$mg\ kernel^{-1}$
Exp. 1	1965	1996–97	11.1	1083	2525	0.43	3194	296
	1982	1996–97	11.8	1175	3001	0.39	3870	255
	1978	1996–97	12.4	978	2395	0.36	4564	256
	1993b	1996–97	10.2	1394	2715	0.51	5856	243
	1993a	1996–97	9.9	1322	2621	0.50	4714	286
Exp. 2	1982	1998–99	9.7	971	2396	0.41	5048	241
	1978	1998–99	10.9	989	2203	0.45	4847	253
	1993b	1998–99	10.8	1344	2605	0.52	7033	224
	1993a	1998–99	10.1	1254	2368	0.53	5629	267
Exp. 3	1993a	2009–10	15.5	1251	2514	0.50	4866	241
	2000	2009–10	13.3	1337	2653	0.50	5322	265
	2005	2009–10	10.1	1381	2605	0.53	5344	259
	2010	2009k10	13.8	1361	2663	0.51	5573	248
Exp. 4	1993a	2010–11	14.7	1345	2661	0.51	5439	261
	2000	2010–11	14	1376	2522	0.55	5587	260
	2005	2010–11	11.7	1456	2784	0.52	6662	242
	2010	2010–11	14.9	1521	2961	0.51	6358	241
Exp. 5	1965	2011–12	12.1	1206	2735	0.44	4005	293
	1993a	2011–12	12.5	1453	2805	0.52	4776	284
	2010	2011–12	16.4	1604	3141	0.51	5982	244

3. Results

3.1. Optimum plant density, yield potential, its determinants and its numerical components

The wide range of plant densities used in this study along with the modified version of Sarlangueís model (Sarlangue et al., 2007) allowed for accurate estimates of grain yield across plant densities (Fig. 1b). Fig. 1 shows an example of the fitted equations to the relationships between Y and D for the hybrid DK664 in Exp. 2. All fitted equations were significant ($p < 0.05$) with R^2 greater than 0.90, for each hybrid × experiment combination (not shown). Optimum plant density (D_{op}) ranged from 9.7 to 16.4 pl m^{-2} (Table 4); and it did not present a clear trend with the year of the hybrid release ($p > 0.05$).

Yield potential increased 0.83% yr^{-1} or 107 kg ha^{-1} yr^{-1} between 1965 and 2010 ($p < 0.05$; Fig. 2). A straight line provided the best fit to the relationship between grain yield and year of hybrid release. Nevertheless, three periods with distinctive rates of grain yield gains were evident ($p < 0.0001$). Hence, rates of grain yield potential increase were (i) close to zero between 1965 and 1982, (ii) 1.69% yr^{-1} between 1982 and 1993, and (iii) 0.55% yr^{-1} between 1993 and 2010 (Fig. 2).

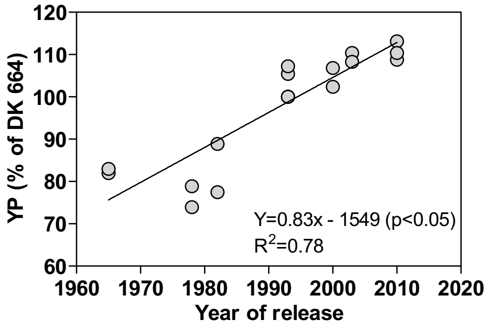

Fig. 2. Yield potential with respect to yield potential of hybrid DK664 (YP, %) as a function of the year of release, for 8 hybrids in Exps. 1–5. The slope of the relationship is the average change per year (%).

Biomass production and HI increased with the year of hybrid release (Fig. 3). Biomass production constantly increased at a rate of 0.35% yr^{-1} or 96 kg ha^{-1} yr^{-1} between 1965 and 2010 (Fig. 3a). Harvest index increased 0.6% yr^{-1} or 0.0031 yr^{-1} during the same period; however, the increment was abrupt between 1982 and 1993 (Fig. 3b). Kernel number per unit area consistently increased

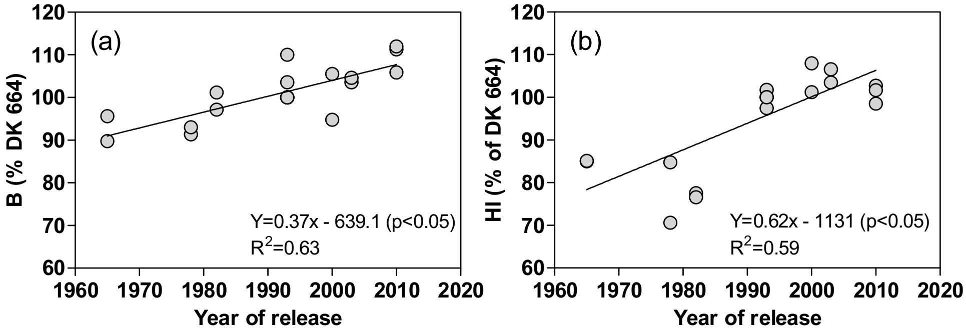

Fig. 3. (a) Shoot biomass per unit area at D_{op} (B, estimated from Eq. (1)) and (b) Harvest Index (HI) at D_{op}, as a function of the year of hybrid release; for 8 maize hybrids in Exps. 1–5. Values were relativized with respect to the mean values of hybrid DK664 (DK664 = 100%); and the slope of the relationship was the average change per year (%).

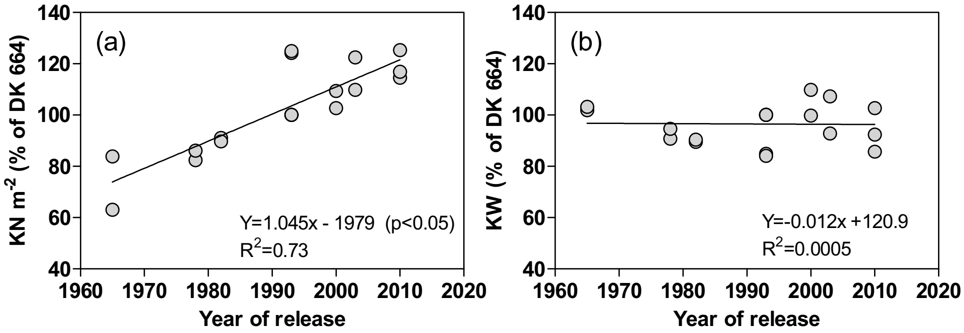

Fig. 4. (a) Kernel number per unit area at D_{op} (KN) and (b) kernel weight at D_{op} (KW) as a function of the year of hybrid release, for 8 hybrids in Exps. 1–5. Values were relativized with respect to the mean values of hybrid DK664 (DK664 = 100%); and the slope of the relationship was the average change per year (%).

at a rate of 0.87% yr^{-1} or 53 kernels m^{-2} yr^{-1} from 1965 to 2010 ($p < 0.05$; Fig. 4a); whereas kernel weight remained unchanged over the years and averaged 258 mg $kernel^{-1}$ among hybrids (Fig. 4b).

3.2. Yield stability and tolerance to high plant density

The trials conducted at 18 locations along with the five hybrids tested at each location provided a wide range of grain yields and environments (Fig. 5). The environmental index (EI) ranged from 5.34 to 11.48 Mg ha^{-1}; and grain yield variability across EI and hybrids was mostly explained by genotype (45.9%) and environment (40.5%) effects; whereas GxE interaction explained 6.4% of the grain yield variation across environments ($p < 0.05$).

Hybrids released in different decades were classified according to the stability analysis method proposed by Finlay and Wilkinson (1963). Thus, (i) the oldest hybrid DKF880 was classified as adapted to low yield environments (i.e. low slope and low mean grain yield); this hybrid, however, had the lowest yield in all environments; (ii) hybrids released in 1993 (DK664 and DK752) were classified as adapted to all environments and with an intermediate stability (i.e. slope close to 1 and intermediate mean grain yields); and (iii) modern hybrids (DK692 RR2 and DK7210 VT3P) were classified as well adapted to high productivity environments but with low stability (i.e. slope greater than 1 and high grain yields; Table 5; Fig. 5a and Fig. 6a); these hybrids, however, presented the highest grain yield at all environments.

Yield stability across environments was also characterized by plotting grain yield of each hybrid as a percentage of EI, according to Tester and Langridge (2010), (Fig. 5b). The slopes of the linear relations were not different from 0 in any hybrid; therefore, grain yield as a percentage of EI did not change across EI. Mean grain yields as a percentage of EI were 57%, 96%, 95%, 116% and 135% for hybrids released in 1965, 1993a and b, 2010 and 2012, respectively (Least significant difference was 7.07%).

According to Francis and Kannenberg (1978) stability analysis method, average grain yield was higher and CV across environments was lower in modern compared with older hybrids (Table 5). Mean grain yield increased from 4518 to 10490 kg ha^{-1} and CV decreased from 33 to 22% with the year of the hybrid release ($p < 0.05$; Table 5; Fig. 6b).

Yield reductions as plant density increased from D_{op} to $2D_{op}$ were lower in modern than in older hybrids (Fig. 7). Grain yield reductions when doubling plant density were 8300 kg ha^{-1} (i.e. 75% of its yield potential) for the oldest hybrid and 1200 kg ha^{-1} (i.e. 8% of its yield potential) for the hybrid released in 2010. In agreement, quadratic coefficients β_2 of the equation fitted to the relationship between relative grain yield and density were less negative in modern than in older hybrids (Fig. 7b).

Grain yield at $2D_{op}$ was closely related to the average grain yield in the five low yielding environments (i.e. environments with EI < 7.2 Mg ha^{-1}) for the four hybrids (DKF880, DK664, DK752 and DK692, Fig. 8a). Grain yield reductions in response to doubling plant density from D_{op} and the CV were significantly and positively associated (Fig. 8b). In agreement, B_2 and CV were closely and negatively associated (Fig. 8c).

4. Discussion

4.1. Yield potential

In Argentina, optimum densities to attain yield potential averaged 12.3 pl m^{-2}, in agreement with previous reports for Argentinean Hybrids (Hernández et al., 2014; Sarlangue et al., 2007). However, optimum densities for yield potential did not present a clear trend with the year of hybrid release, in contrast with reports from other countries (Derieux et al., 1987; Duvick, 2005; Tollenaar, 1989). Similar results were obtained with Duncan (1958) methodology (not shown).

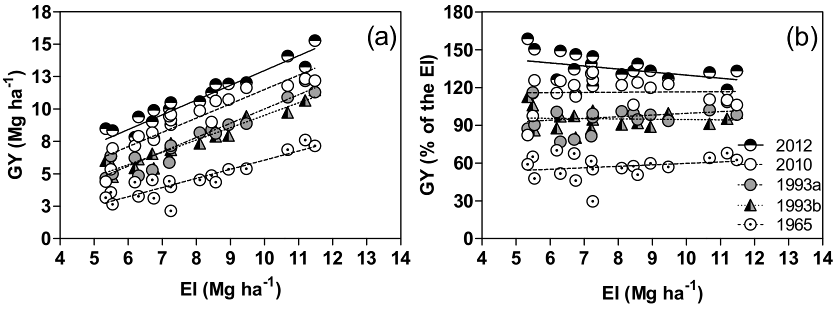

Fig. 5. (a) Grain yield (Y, Mg ha^{-1}) as a function of the Environmental Index (EI). Each line represents the linear regression for each genotype and coefficients are presented in Table 5. (b) Grain yield relativized with respect to EI at each location (Y, %) as a function of EI. Data correspond to 5 hybrids released between 1965 and 2012, in Exp. 6.

Table 5
Average grain yield across environments (GY $\dot{X}$), coefficient "CV" (Francis and Kannenberg, 1978), coefficient "b" (Finlay and Wilkinson, 1963), confident interval of "b" (CI), intercept and R^2 of the regression, for 5 hybrids released between 1965 and 2012, in Exp. 6.

Year of hybrid release	GY $\dot{X}$ (Mg ha^{-1})	Francis and Kannenberg	Finlay and Wilkinson			
		CV	b	CI (95%)	Intercept	R^2
1965	4.52	33.7	0.71	0.62–0.79	−1.007	0.80
1993b	7.44	25.7	0.95	0.88–1.02	−0.021	0.92
1993a	7.60	29.4	1.10	1.00–1.19	−1.009	0.90
2010	9.10	25.1	1.10	0.99–1.21	0.472	0.87
2012	10.49	22.0	1.14	1.05–1.23	1.570	0.91

All fitted regressions were significant ($p < 0.0001$).

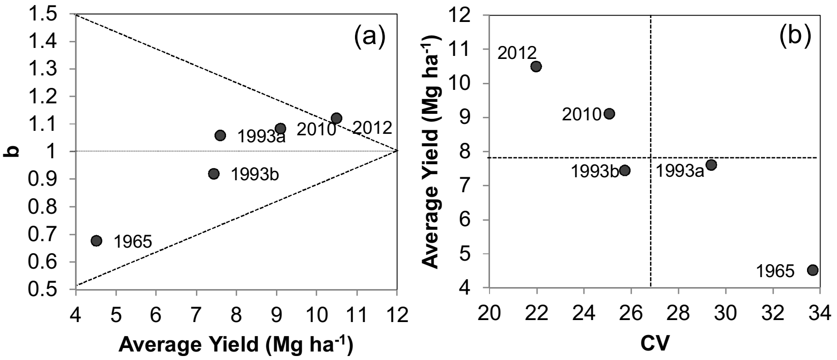

Fig. 6. (a) Coefficient "b" (; Finlay and Wilkinson (1963) as a function of average Y across environments in Exp. 6. Dashed lines indicate the classical division of Finlay and Wilkinson (1963). (b) Average Y across environments as a function of the coefficient of variation (CV; Francis and Kannenberg, 1978). Dashed lines indicate mean value of average yield and of CV. Data correspond to 5 hybrids released between 1965 and 2012, in Exp. 6.

Maize yield potential increased from 1965 to 2010 (Fig. 2), and kernel number was the main yield numerical component contributing to explain the increase in yield potential (Echarte et al., 2000; Otegui, 1995). Most of the hybrids used in this study were developed by one seed company (i.e. Dekalb-Monsanto); however, based on that (i) these hybrids were among the most cultivated hybrids at the time of their release, (ii) the high level of participation of Dekalb-Monsanto in the Argentinean market, and (iii) the similar mean grain yield trends between Dekalb-Monsanto and Argentina maize production in the period 1980–2010 (Mastronardi, 2012); it is expected that results from this retrospective study contribute to reflect the maize yield potential trends in Argentina during the last 45 years.

Average rate of yield potential improvement was 107 kg ha^{-1} yr^{-1} between 1965 and 2010 (i.e. average rate of 0.83% yr^{-1}; Fig. 2). This rate is lower than those previously published (Echarte et al., 2004; Luque et al., 2006). Differences might be attributed to the comparison of hybrids at their optimum plant density and to the inclusion of hybrids released during the last two decades in this study. In the first period from 1965 to 1982, the rate of yield improvement was the lowest and it was negligible; this was probably attributed to the use of double cross hybrids, which were characterized with a high plant to plant variability and a low HI (Echarte and Andrade, 2003). The highest rate of yield improvement, which occurred from 1982 to 1993 (i.e. 1.69% yr^{-1}), was likely associated to the introduction of single cross maize hybrids. It has been shown that single cross hybrids may yield on average 10% more than double crosses (Weatherspoon, 1970). In accordance, Troyer, (1996) reported lower rates of yield improvement in double than in single cross hybrids. Grain yield advantages of single cross hybrids were associated with greater kernel number per plant, lower plant to plant variability and higher HI than double cross maize hybrids (Echarte and Andrade, 2003; Echarte et al., 2004). In this period, HI increased from 0.4 to 0.52 (Fig. 3b) and it was closely associated with the grain yield improvements from 1982 to 1993. Yield potential increments occurred at a lower rate from 1993 to 2010 (i.e. 0.55% yr^{-1}; Fig. 2). In accordance, trends in mean yield plateaus or desacelerated yield increments after 1990 were also observed for maize, wheat and rice in different countries (Grassini et al., 2013). Yield potential increments during this period were mainly associated with increments in biomass production (Fig. 3a). Harvest index remained stable during the last two

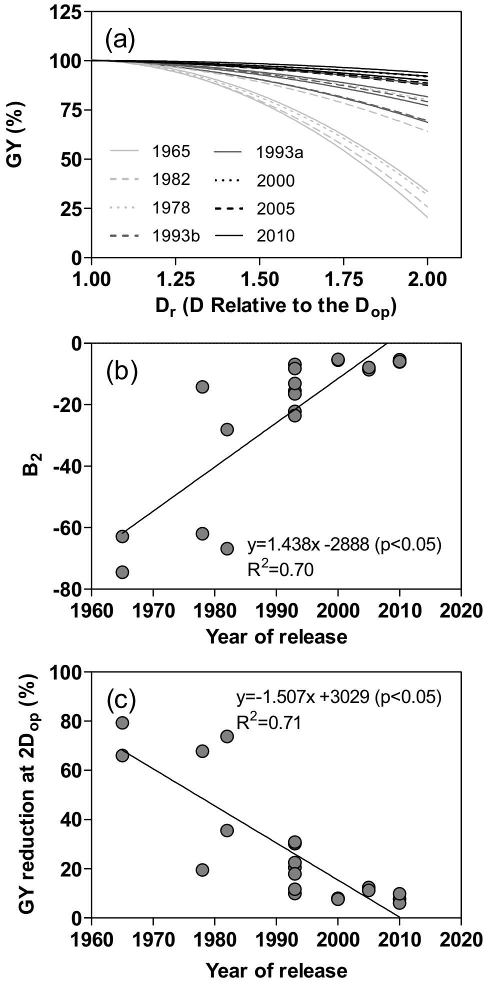

Fig. 7. (a) Grain yield relative to yield at D_{op} (%) in response to plant density increments from D_{op} = 1 to $2D_{op}$ = 2. Each line is the quadratic relationship fitted to the Y obtained using Eq. 4. (b) Coefficient B_2 of the quadratic functions in Fig. 7a and (c) grain yield reduction (%) in response to doubling D_{op} as a function of year of hybrid release. Data correspond to 8 hybrids in Exps. 1–5.

decades; associated likely with poor improvements in dry matter partitioning to the ear during the critical period for kernel set. In addition, yield increments accompanied with increments in shoot biomass were required in order to prevent from a more deteriorated source-sink ratio in current maize hybrids (Cerrudo et al., 2013; Echarte et al., 2006). Interestinlgy, HI also remained stable around 0.52 in EEUU during the period between 1930 and 2001 (Duvick, 2005) and during 1959–1988 in Canada (Tollenaar, 1989); and HI increments across decades were found only under resource limiting conditions (i.e. at high densities for hybrids in EEUU, (Duvick et al., 2004) or with a set of populations of maize under drought stress conditions, (Edmeades et al., 1999). These data together would indicate that HI is approaching an upper limit close to 0.52 for maize hybrids grown in optimum conditions (i.e. 48% of the total shoot biomass is the minimum source required to support grain yield production); thus, future yield gains seems only be possible by further shoot biomass production increments. In accordance, upper limits in HI were reported for other crops during the last decades; for example for wheat, barley and rice (Hay, 1995). To the best of our knowledge, there is no published information about the theorethical limit of HI in maize. Further studies about the physiological mechanisms contributing to yield improvements during the last two decades are currently ongoing.

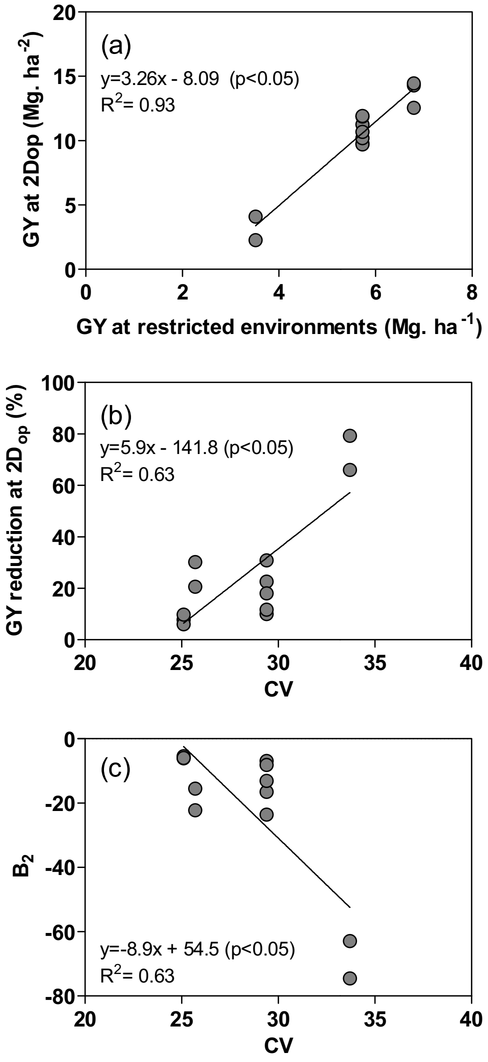

Fig. 8. (a) Grain yield at $2D_{op}$ (Y, Mg ha^{-1}; estimated from Eq. (4)) as a function of Y at the 5 most restricted environments (from Exp. 6). (b) grain yield (Y) reduction to doubling D_{op} (%, from Eq. (7)) and (c) B_2 from Eq. (9), as a function of CV (Francis and Kannenberg, 1978). In Fig. 8a each value of Y at restricted environments and in Fig. 8b and c, each value of CV corresponds to one hybrid released between 1965 and 2010 in Exp. 6 and each value of Y at $2D_{op}$ (a) Y reduction at $2D_{op}$ (b) or B_2 (c) corresponds to one hybrid x experiment combination (i.e. two experiments for hybrids DKF880 and DK752, three experiments for DK692 and five experiments for hybrid DK664). Only data for the hybrids that appears in both analyses (i.e. yield stability and tolerance to high plant densities) were used.

4.2. Yield stability

Two approaches were used to test for yield stability across environments (i.e. Finlay and Wilkinson, 1963 and Francis and Kannenberg, 1978). According to Finlay and Wilkinson (1963) stability method, a coefficient *b* greater than 1 classified modern maize hybrid as well adapted to high yielding environments but with low stability. Coefficient *b*, however, does not contemplate the larger grain yield of modern compared with older hybrids in all environments. Francis and Kannenberg (1978) method considered mean grain yield and its variation across environments in a single coefficient (CV). This method was able to show a significant CV reduction with the year of the hybrid release (Fig. 6); which was reflecting greater yield stability and also greater average grain yield of modern compared with older hybrids. Thus, this analysis demonstrated the superiority of modern hybrids in low yielding environments; which is in accordance with the greater yield gains with the year of hybrid release, in poor environments (i.e. ≈2% yr^{-1}, in environments with EI < 6 Mg ha^{-1}) than in rich environments (i.e. ≈1% yr^{-1}, in environments with EI > 11 Mg ha^{-1}; from Fig. 5a).

The greater yield stability of modern maize hybrids might be attributed in part to the introduction of North American background in the early 1980s in Argentina; and also to the testing of hybrids performance in a wide range of locations. Breeding programs in Argentina have developed the hybrids used in this study and the testing of advanced hybrids is currently done in more than 150 locations (de Santa Eduviges, 2010; Eyherabide and Damilano, 2001). Similarly, US advanced hybrids were tested in 15–40 locations in the 1960s and the number of locations increased to 100 in the 1990s in EEUU (Troyer, 1996).

4.3. Tolerance to high plant densities

Plant density increments from D_{op} to two times D_{op} (i.e. $2D_{op}$) promoted lower grain yield reductions in modern compared with older hybrids (Fig. 7), in agreement with reports for hybrids released in EEUU (Duvick et al., 2004). In accordance, the gain in yield with the year of hybrid release was larger at high plant densities (i.e. 2.13% yr^{-1} at $2D_{op}$, $p < 0.0001$) than at D_{op} (0.83% yr^{-1} at $D_{op;}$ $p < 0.0001$; from Fig. 7a). Thus, it was evident that tolerance to high plant density increased with the year of hybrid release (Fig. 7).

The lower threshold of Bp for yield production of current maize hybrids (i.e. *Bt*, Eq. (2); not shown) supports their greater tolerance to high plant densities compared with older hybrids; in accordance with results from Echarte and Andrade (2003) in a study with hybrids released between 1965 and 1993. A greater high plant density tolerance might be associated with less kernel abortion per uppermost ear and/or less number of barren plants. Previous studies have demonstrated that hybrids released in 1993 were able to set more kernels in the uppermost ear per unit plant growth rate during the critical period for kernel set (i.e. 30 days bracketing silking; PGR) than hybrids released in 1965 (Echarte et al., 2000; 2004). Further, greater kernel set per unit PGR might be attributed to (i) lower threshold of PGR for kernel set (Echarte et al., 2004); (ii) less plant to plant variability in PGR (Maddonni and Otegui, 2006) and/or (iii) the maintenance of a greater PGR (Echarte et al., 2004).

4.4. Tolerance to high plant densities as a surrogate of yield stability

Yield stability and tolerance to high plant density increased with the year of hybrid release (Fig. 6b and Fig. 7); and there was a significant direct association between tolerance to high plant densities and yield stability (i.e. hybrids with high tolerance to high plant densities were stable across environments; Fig. 8). Thus, tolerance to high plant density could be a surrogate of stress tolerance in the field. These results provide strong bases for the use of high plant densities as a breeding technique (Dow et al., 1984) in order to obtain yield stability. With this purpose, breeding programs in Argentina began to test hybrids at high plant density in the 1990s. Previous works have speculated with the association between both traits (e.g. Tollenaar and Lee, 2002) or have indicated that there are common mechanisms underlying tolerance to different type of stresses (Bänziger et al., 2002; Andrade et al., 2002; Dow et al., 1984). The association between yield stability across environments and tolerance to high plant density in maize is based on the fact that the reduction in resource availability per plant at high plant density, which reduces dry matter partitioning to the ear at flowering, represents the effect of different types of stresses at the crop level. The physiological mechanisms underlying tolerance to high plant densities and yield stability will be the focus of future studies.

5. Conclusions

This study have presented novel findings regarding the trends in optimum plant density and in yield potential and its components for maize hybrids released in Argentina between 1965 and 2010. It was demonstrated that optimum plant density ranged from 9.7 to 16.4 pl m^{-2} and that there was not a clear trend in optimum plant density for hybrids released between 1965 and 2010. However, yield potential (i.e. grain yield at the optimum plant density for each hybrid) consistently increased at a rate of 0.83% yr^{-1} or 107 kg ha^{-1} yr^{-1} during the same period. This increment was attributed to steady increments of biomass production during the whole period (1965–2010) and to abrupt increments in HI from 1982 to 1993. Harvest index has remained unchanged at 0.52 during the last two decades for maize hybrids grown in optimal conditions.

Results of this work demonstrated also, that tolerance to high plant density consistently increased from 1965 to 2010. In a separate set of trials that included a wide range of environments, it was shown that yield stability increased during the last 45 years. A distinctive finding of this work was the significant and direct association between tolerance to high plant density and stability across environments providing strong bases for the use of high plant densities as a method to attain gains in yield stability.

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